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MORPHOLOGY OF THE DORSAL INTEGUMENT OF TEN OPILIONID SPECIES (ARACHNIDA, OPILIONES)

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ABSTRACT

Specimens of *Siro exilis* Hoffman, *Vonones sayi* (Simon), *Erebomaster* sp., *Leiobunum vittatum* (Say), *Leiobunum holtae* McGhee, *Hadrobunus maculosus* (Wood), *Eumesosoma nigrum* (Say), *Odiellus pictus* (Wood), *Caddo agilis* Banks, and *Hesperonemastoma kepharti* (Crosby and Bishop) were investigated using scanning electron microscopy. Features of the dorsal integument of each specimen are described using available terminology. Variations in the generalized tuberculate-granulate morphology were observed in eight of the ten species studied. *V. sayi, C. agilis*, and *O. pictus* exhibit a morphological gradient in features of their dorsal integuments. The presence of micropores is reported from the apices of tubercles of *L. vittatum, L. holtae, H. maculosus*, and *O. pictus* and from the cuticular backgrounds of *S. exilis, V. sayi*, and *E. nigrum*. The morphological descriptions and comparisons presented provide a terminology for describing opilionid cuticular features.

INTRODUCTION

Species of the order Opiliones are often characterized by prominent protuberances, spines, and ornamented cuticles, especially in the suborder Laniatores (Shear and Gruber 1983). Studies with scanning electron microscopy (SEM) reveal still other, smaller, cuticular features. In the past, morphological studies of arthropod integuments have been primarily limited to insects. Although various morphological descriptions of the arachnid cuticle exist in the literature, a consistent descriptive terminology is currently unavailable.

Previous light microscopical studies of arachnid integuments include those of Edgar (1963), Immel (1964), Grainge and Pearson (1966), Kennaugh (1968), Dalingwater (1975, 1981, 1987), and van der Hammen (1985), among others. Selected SEM studies of arachnid taxa exclusive of the Opiliones include those of Brody (1970), Pittard and Mitchell (1972), Woolley (1974), Crowe (1975), Quintero (1975), Platnick and Gertsch (1976), Platnick and Shadab (1976), Mutvei (1977), Keirans and Clifford (1978), Hill (1979), Hadley and Filshie (1979), Emerit (1981), Hadley (1981), Opell (1983), Platnick (1986), and Igelmund (1987). SEM studies of various opilionid species were conducted by Juberthie and Massoud (1976), Martens (1979), Martens and Schawaller (1977), and Spicer (1987). Martens (1978) referred to both macro- and micromorphological features

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of the opilionid integument. Shear (1986) and Shear and Gruber (1983) used SEM to illustrate characters for cladistic analysis of ischyropsalidoid and troguloid opilionids.

The purpose of this paper is to illustrate the cuticular features of ten opilionid species, propose a descriptive terminology for these features, and make preliminary comparisons of related species based on their cuticular features.

METHODS AND MATERIALS

Sources of material.—Specimens were obtained from the private collection of Dr. Charles R. McGhee at Middle Tennessee State University and from localities in Rutherford, Bedford, Cannon, McMinn, and Hickman counties of Tennessee. One species, *Eumesosoma nigrum* (Say), was on loan from the American Museum of Natural History.

Method of study.—All specimens were preserved in 70% ethanol prior to preparation for SEM. The specimens were allowed to air dry or were freeze-dried from quick-frozen distilled water using a Thermovac lyophilizer. Freeze-drying was used for those species whose cuticles became distorted with air desiccation.

The dried specimens were mounted on aluminum stubs using an epoxy glue for larger specimens and double-stick adhesive tape for smaller specimens, coated with gold-palladium in a Technics Hummer VI sputtering system, and examined at an accelerating voltage of 15 kV in an ISI SX-30 SEM. Photomicrographs were made with a Pentax MX 35 mm camera using Kodak™ Plus-X film.

The surface features illustrated by the photomicrographs were compared with existing micrographs and morphological descriptions of both arachnid and insect integuments in an attempt to apply an appropriate descriptive terminology. The investigations of Harris (1979), Byers and Hinks (1973), Hinton (1970), and Kennaugh (1968) as well as the general works of Torre-Bueno (1962), Steinmann and Zombori (1981), and Baker and Wharton (1952) were used as primary sources of descriptive terminology.

Magnification and terminology.—The photomicrographs are reproduced at magnifications which best illustrate the proposed terminology. Measurements in micrometers (um) are given to provide size comparisons.

Because many descriptive terms exist with both diminutive and superlative forms, micromorphological descriptions require standards for selecting proper terms. The author agrees with Shear and Gruber (1983) who used the prefix "micro-" preceding terms describing features which measure 0.01 mm or less in size. Often, a species' integument is sufficiently detailed to warrant the use of two, rarely three, descriptive components. This procedure is favored over the arbitrary creation of terms in a field often burdened with excessive synonymy.

RESULTS

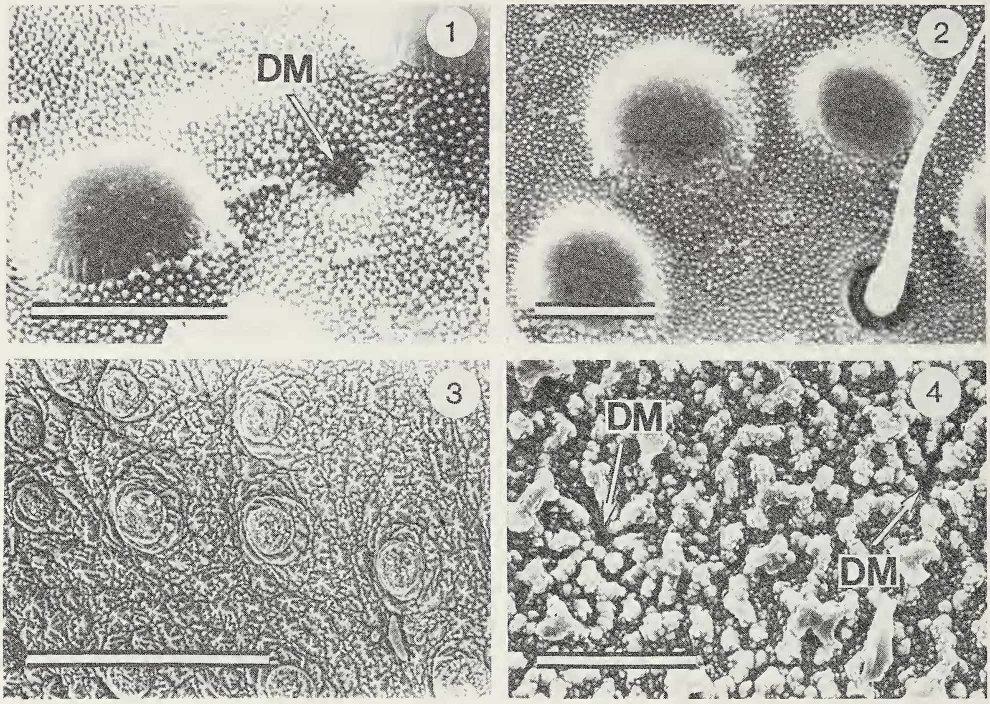
The features of the dorsal integument of ten opilionid species representing nine genera and six families within the three suborders of the Opiliones were examined and described (Table 1). No cuticular differences attributable to sexual dimorphism were observed in species for which both sexes were available for study. A systematic list of the species studied is given in Appendix 1. Cuticular

Table 1.—A summary of the cuticular features of 10 opilionid species. Refer to Appendix 1 for higher taxonomy.

	S. exilis	*V. sayi*	*E.* sp.	*L. vitt.*	*L. holt.*	*H. mac.*	*E. nig.*	*O. pic.*	*C. agilis*	*H. kepharti*
Tuberculate	X	X		X	X	X	X	X		
Convex	X									
Rounded				X	X	X		X		
Basally constricted							X			
Microgranulate		X								
Laminate				X	X	X		X		
Spirally				X	X	X				
Perpendicularly								X		
Glabrous								X		
Microtuberculate			X						X	X
Convex			X							
Oblong										X
Obtuse/subdeltoid									X	
Reticulate			X							
Microgranulate										X
Denticles						X				
Micropores	X	X					X	X		
On tubercles				X	X	X		X		
Not on tubercles	X	X					X			
Foveolate	X	X					X			
Cycloid facetodea		X	X			X		X	X	
Micrograpnulate	X	X	X	X	X	X	X			X
Two-ranked	X									
Dentate				X	X	X	X			
Imbricate		X						X	X	
Subimbricate		X							X	
Laminate		X						X		
Acute/obtuse		X						X		
Keeled		X						X		
Mucronate								X		
Reticulate								X		
Rivulose		X	X							
Rugose-plicate									X	
Sinuate		X								
Striate									X	
Rectilinear setae	X		X							
Arcuate setae		X		X	X	X	X	X	X	X
Substriate setae		X		X	X	X	X		X	X
Spirally		X		X	X	X	X		X	X
Setae on areolae		X	X							
Torose areolae		X								
Setae on microareolae				X	X	X	X		X	X
Rounded				X	X	X				X
Depressed							X		X	
Setae on microalveolae	X									

comparisons between related species (see Discussion) are made to better distinguish the characters of each species and are not intended to show phylogenetic relationships. Applied descriptive terminology is defined in Appendix 2.

Siro exilis **Hoffman.**—*Dorsal integument:* A tuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 1). The convex tubercles are smooth above with abbreviated



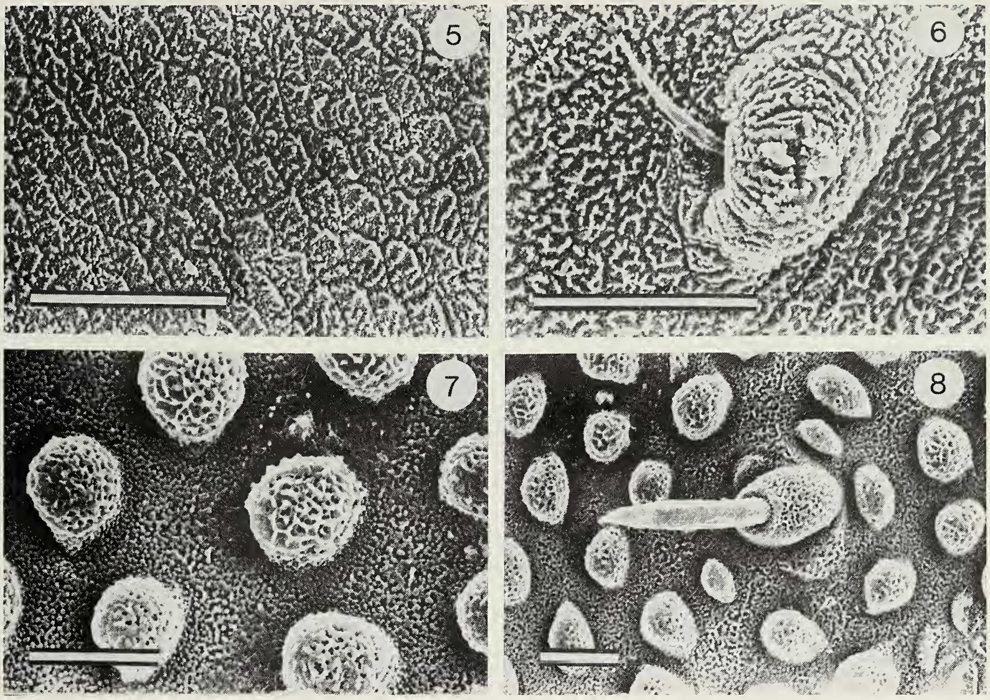
Figs. 1-4—Opilionid dorsal integument morphology: 1-2, *S. exilis*; 1, dermal gland micropore (DM); 2, abdominal seta; 3-4, *V. sayi*, 3, anterior cephalothorax; 4, posterior cephalothorax with dermal micropores. Scale = 10 μm, except Fig. 3, 100 μm.

microstriae surrounding their bases. The microgranulations of the cuticular background are regularly spaced, two-ranked, and appear as rounded points. The larger microgranulations measure 0.5 μm in basal diameter and as many as 40 are present in a given 25 μm^2. The smaller microgranulations measure 0.25 μm in basal diameter and as many as 70 are represented in 25 μm^2. The openings of dermal gland micropores (Juberthie and Massoud 1976) are seen as microfoveolae (Fig. 1). Each opening is encircled by 15-17 of the larger microgranulations.

Abdominal setae: Rectilinear-acicular setae arise from depressed microalveolae (Fig. 2).

Vonones sayi **(Simon).**—*Dorsal integument:* The anterior cephalothoracic region exhibits a tuberculate-rivulose-microgranulate morphology (Fig. 3). The tubercles are located anterior to the ocularium and appear as rounded microgranular elevations of the cuticle. No micropores are visible on the surfaces of the tubercles. The cuticular surface has a subimbricate background of polygonal plates which exhibit a pattern of microgranular, sinuate furrows. The furrows are in relief of non-parallel ridges formed by fusion of the microgranulations. Numerous micropores appear as foveolae and are encircled by microgranulations. The microgranulations vary considerably in size and shape, with a maximum basal diameter of 0.4 μm.

Both the posterior cephalothoracic and anterior abdominal regions exhibit a rivulose-microgranulate morphology (Fig. 4) which closely resembles that of the anterior cephalothorax, with the exception that no tubercles or polygonal plates are seen. The openings of micropores are also seen in this region.



Figs. 5-8—Opilionid dorsal integument morphology: 5-6, *V. sayi*; 5, posterior abdomen; 6, cephalothoracic seta; 7-8, *Erebomaster* sp.; 7, dorsum; 8, abdominal seta. Scale = 50 μm (Figs. 5-6), 10 μm (Figs. 7-8).

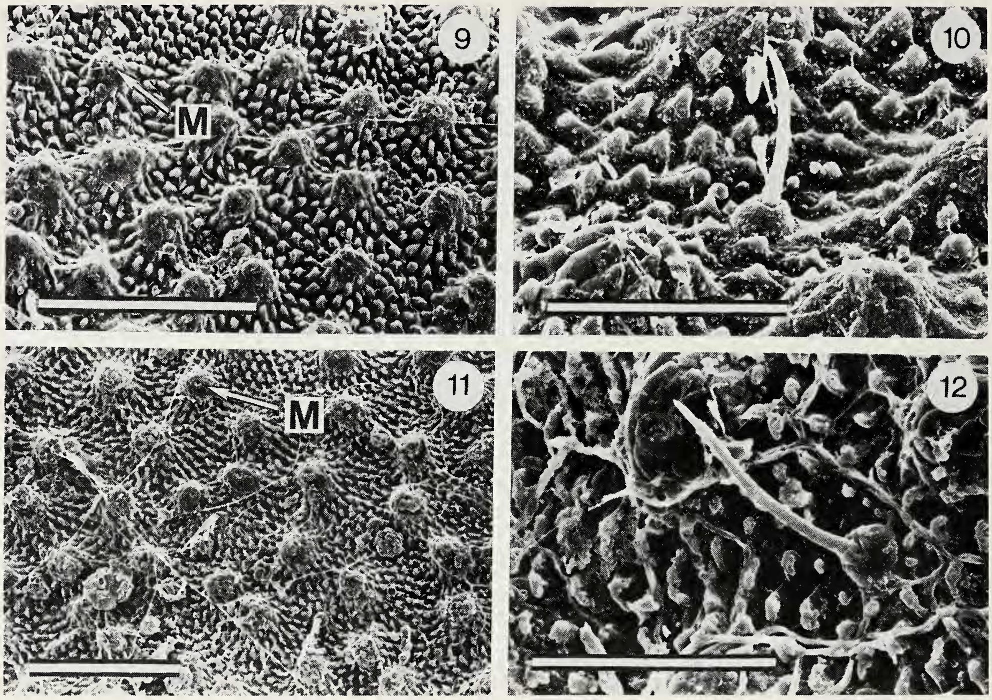
The posterior abdominal region of *V. sayi* is imbricate-rivulose-microgranulate (Fig. 5). The imbrications or laminae are essentially similar to the polygonal plates of the anterior cephalothoracic region. The laminae are, however, keeled distally and range from obtuse to acute. Micropores also are seen in this region.

Cephalothoracic setae: Arcuate-acicular setae lie parallel to the surface of the integument (Fig. 6). The setae are spirally substriate with basal, torose areolae which are rivulose-microgranulate. Setae are found only in the lateral areas of the cephalothorax, in certain areas of the posterior abdomen, and on the appendages.

***Erebomaster* sp.**—*Dorsal integument:* A microtuberculate-rivulose-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 7). The numerous, convex microtubercles are superficially reticulate in some cases while others exhibit a punctulate morphology. The microgranulations of the cuticular background are of variable size and shape and have a maximum basal diameter of 0.1 μm. Abbreviated asymmetrical ridges are formed by fusion of the microgranulations. Micropores, if present, can not be distinguished from either the punctulations of the microtubercles or the coalescent microgranular background.

Abdominal setae: Rectilinear, thick-shafted setae lie parallel to the surface of the integument (Fig. 8). The setae have prominent basal areolae which, like the microtubercles, are rivulose-microgranulate.

***Leiobunum vittatum* (Say).**—*Dorsal integument:* A tuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 9). The tubercles appear as rounded elevations of the cuticle and



Figs. 9-12.—Opilionid dorsal integument morphology: 9-10, *L. vittatum*; 9, micropore (M); 10, abdominal setae; 11-12, *L. holtae*; 11, micropore; 12, abdominal seta. Scale = 50 μm (Figs. 10, 12), 100 μm (Figs. 9, 11).

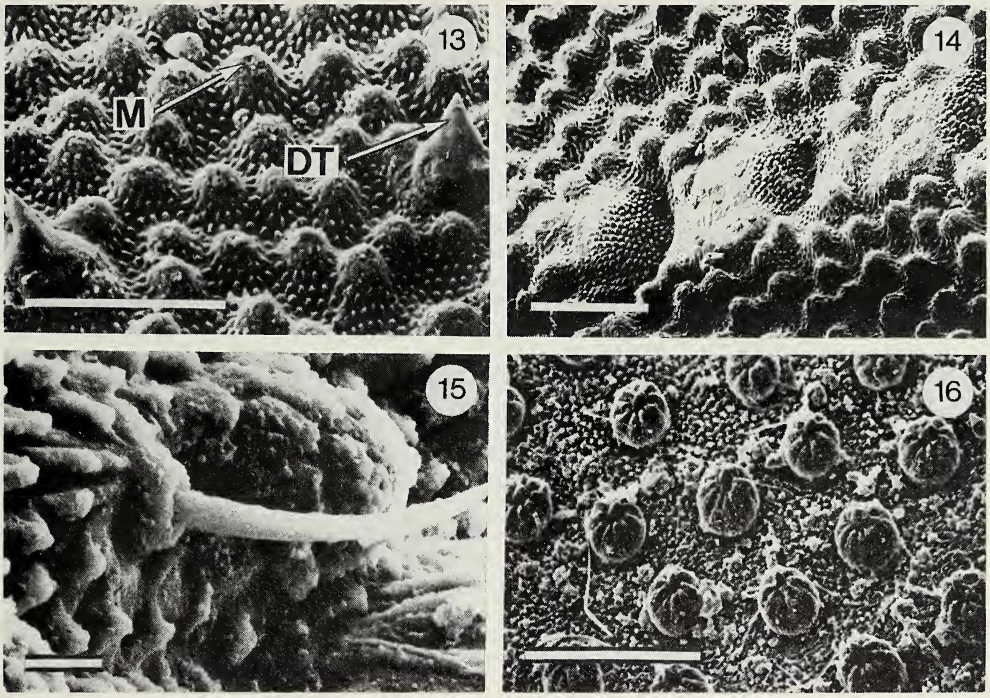
are covered by a number of laminae which form a loosely aggregated spiral. A micropore is visible at the summit of each tubercle. The microgranulations are subequal in size and appear as dentate projections of the integument. The basal width of the microgranulations ranges from 5 to 8 μm. The less sclerotized, transverse and lateral areas of the dorsum are microgranulate and devoid of tubercles.

Abdominal setae: Thick-shafted, arcuate-acicular setae arise from rounded microareolae which do not resemble the larger tubercles or the smaller microgranulations (Fig. 10). The setae are spirally substriate.

***Leiobunum holtae* McGhee.**—*Dorsal integument:* As illustrated in Fig. 11, both the cephalothoracic and abominal tergites of this species are tuberculate-microgranulate. The cuticular morphology closely resembles that of *L. vittatum*. All regions of the dorsal integument of *L. holtae* exhibit both tubercles and microgranulations.

Abdominal setae: As illustrated in Fig. 12, the setae of *L. holtae* closely resemble those of *L. vittatum*.

***Hadrobunus maculosus* (Wood).**—*Dorsal integument:* A tuberculate-microgranulate morphology is exhibited by both the cephalothoracic and abdominal tergites of this species (Fig. 13). The cuticular morphology closely resembles that of the two *Leiobunum* species with the exception of smooth, pointed denticles which are sparsely distributed. The denticles measure approximately 50 μm in height and 40 μm in basal width. Tubercles, denticles, and microgranulations are observed from all regions of the dorsal integument. Numerous circular structures consisting of



Figs. 13-16.—Opilionid dorsal integument morphology: 13-15, *H. maculosus*; 13, micropore (M) and denticle (DT); 14, cycloid facetodea; 15, abdominal seta; 16, *E. nigrum*. Scale = 100 μm, except Fig. 15, 10 μm.

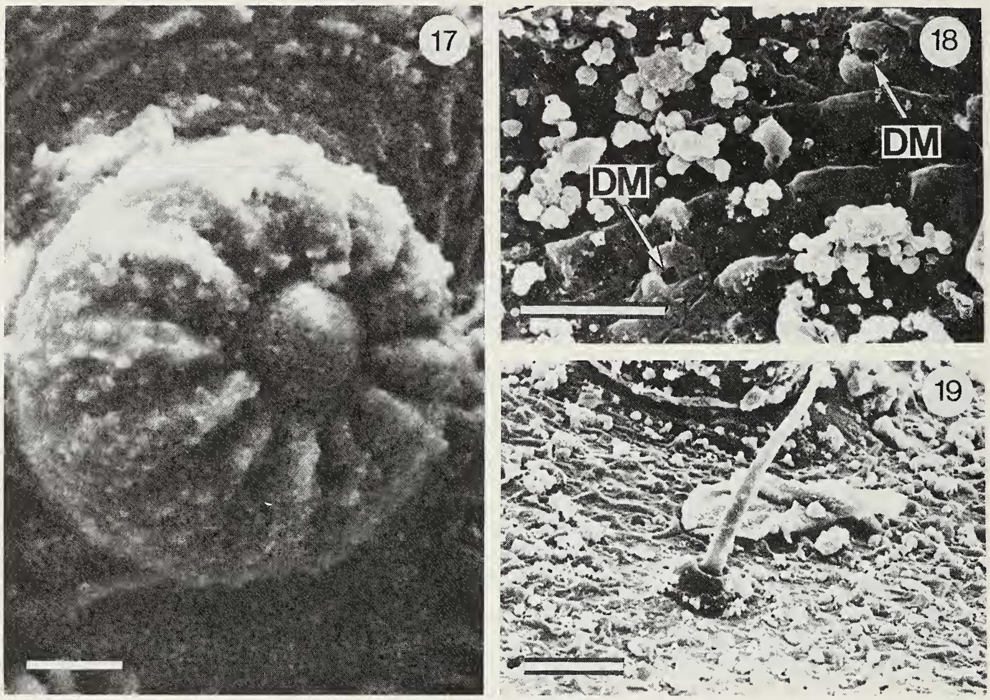
many closely associated papillae range from 50 to 65 μm in diameter and appear in transverse rows across the dorsum (Fig. 14). For the time being, I term these structures "cycloid facetodea" since they resemble the multifaceted compound eyes of insects.

Abdominal setae: As illustrated in Fig. 15, the setae of *H. maculosus* closely resemble those of the two *Leiobunum* species.

Eumesosoma nigrum **(Say).**—*Dorsal integument:* A pronounced tuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 16). The prominent tubercles are subspherical and constricted basally. The tubercles show radial symmetry above with abbreviated striae radiating from a rounded process (Fig. 17). The tubercles measure approximately 40 μm in diameter and 30 μm in height and no micropores are distinguishable above. The microgranulations are of variable size and appear as dentate projections of the integument. The basal width of the microgranulations ranges from 5 to 8 μm. Sparsely distributed micropores appear as microfoveolae and are partially encircled by incomplete microareolae (Fig. 18). The microareolae measure approximately 5 μm in diameter.

Abdominal setae: Arcuate-acicular, thick-shafted setae arise from concave depressions atop rounded microareolae (Fig. 19). The microareolae do not resemble the other cuticular features and range from 7 to 9 μm in diameter. The setae are spirally substriate.

Odiellus pictus **(Wood).**—*Dorsal integument:* The cephalothoracic region of *O. pictus* exhibits a tuberculate-imbricate-reticulate morphology (Fig. 20). The



Figs. 17-19.—Opilionid dorsal integument morphology: *E. nigrum*; 17, tubercle; 18, dermal micropores (DM); 19, abdominal setae. Scale = 10 μm.

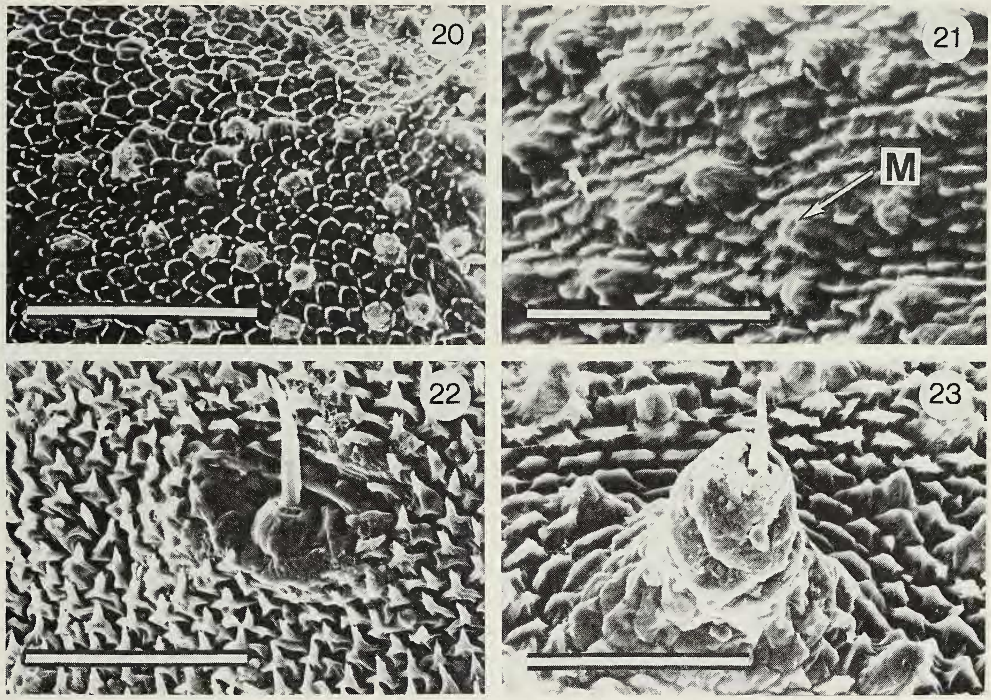
tubercles appear as rounded elevations of the integument, each possessing a micropore at its apex. Most of the tubercles are glabrous above but some are encircled by oblong laminae which are perpendicular to the cuticular surface. The imbrications are distributed as laminae and form a shingle-like arrangement. The distal margins of the laminae range from obtuse to acute. The reticulations appear as marginal elevations of the laminae.

A tuberculate-imbricate morphology is observed from the anterior abdominal region of this species (Fig. 21). The tubercles closely resemble those of the cephalothoracic region. However, the laminae are strongly keeled distally and occur in thickset layers. The distal margins of the laminae are acute.

The posterior abdominal region is imbricate-mucronate (Fig. 22). Tubercles are absent from the last two abdominal segments. The laminae occur in thickset layers and each ends in a fine point or mucro.

Abdominal setae: Two types of arcuate-acicular, thick-shafted setae are observed from the abdominal region. One form arises from external processes which are much larger than the abdominal tubercles, measuring approximately 40 μm in height and 35 μm in basal diameter (Fig. 23). The other type of setae arise from smaller tubercles measuring approximately 12 μm in both height and basal diameter (Fig. 22). Each of these seta-bearing tubercles is located within an incomplete alveolus and is subparallel to the surface of the integument.

***Caddo agilis* Banks.**—*Dorsal integument:* A subimbricate-microtuberculate morphology is observed from the cephalothoracic region, particularly the ocularium of this species (Fig. 24). The surface of the integument has a subimbricate background of polygonal plates and microtubercles of variable size.



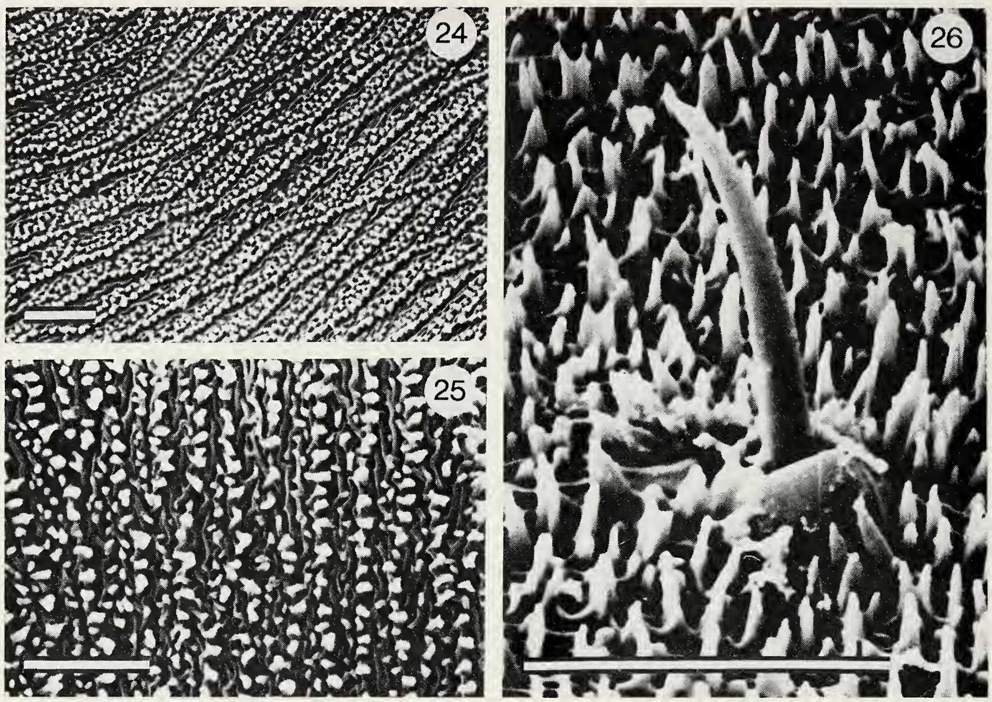
Figs. 20-23.—Opilionid dorsal integument morphology: *O. pictus*; 20, cephalothorax; 21, anterior abdomen showing micropore (M); 22, posterior abdomen and seta; 23, abdominal seta. Scale = 50 μm, except Fig. 20, 100 μm.

The larger microtubercles range from obtuse to subdeltoid and line the distal margins of the imbrications. Numerous smaller, obtuse microtubercles cover each of the polygonal imbrications. No micropores are observed from any region of the dorsum.

The abdominal region of *C. agilis* is rugose-plicate-microtuberculate (Fig. 25). The microstructure of the integument resembles that of the cephalothoracic region with the exception that the polygonal imbrications are not present. The cuticular surface exhibits a folded pattern of impressed striae in relief of torose plications. The microtubercles closely resemble those of the cephalothoracic region and project from the plications at irregular intervals. The integument of *C. agilis* is more easily distorted when desiccated prior to SEM than that of the other species examined.

Abdominal setae: Thick-shafted, arcuate-acicular setae arise from rectangular depressions atop microareolae (Fig. 26). The mcroareolae range from 7 to 9 μm in basal diameter and do not resemble other cuticular features. The setae are spirally substriate.

***Hesperonemastoma kepharti* (Crosby and Bishop).**—*Dorsal integument:* A microtuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 27). The numerous oblong, convex microtubercles exhibit microgranulations above and are constricted basally. A concave depression surrounds the posterior one-half of each microtubercle. The posterior margins of the microtubercles extend over the concave depressions and range from obtuse to acute. In the posterior abdominal



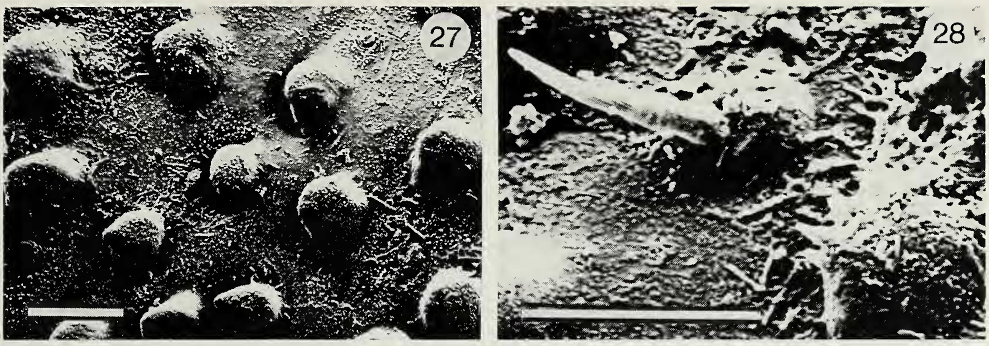
Figs. 24-26.—Opilionid dorsal integument morphology: *C. agilis*; 24, cephalothorax; 25, abdomen; 26, abdominal seta. Scale = 10μm.

region, some of the posterior tubercular margins exhibit a trident of acute microdenticles (Fig. 28). The microgranulations are of variable size and are often sparsely distributed upon primarily glabrous areas of the integument. No micropores are distinguishable from either the surfaces of the microtubercles or the microgranular background.

Abdominal setae: The setae are arcuate-acicular, spirally substriate, and thick-shafted (Fig. 28). They arise from the posterior margins of rounded microareolae at approximately a 45 degree angle to the integument.

DISCUSSION

Juberthie and Massoud (1976) conducted an SEM study of six cyphophthalmid species exclusive of *S. exilis* and reported that the species examined have similar cuticular features. The cuticular morphology of *S. exilis* closely resembles that of the six species studied by Juberthie and Massoud. Variations in cuticular morphology among the Sironidae include differences in the ratios of the two sizes of microgranulations per unit area, variations in the position of dermal gland micropores (e.g., a number of micropores are adjacent to the tubercles in *Metasiro americanus* (Davis)), and differences in the shape and size of the tubercles (Juberthie and Massoud 1976). This indicates that seven of the more than 50 known cyphophthalmid species have the same basic cuticular morphology. Although Shear (1980) did not use cuticular morphology as a taxonomic character in his reclassification of the Cyphophthalmi, further studies of representatives of the related family Pettalidae and superfamilies Stylocelloidea



Figs. 27-28.—Opilionid dorsal integument morphology: *H. kepharti*; 27, dorsum; 28, abdominal seta. Scale = 10 μm.

and Ogoveoidea are needed to determine the importance of integumental microstructure in classifying cyphophthalmids.

The cuticular morphology of *V. sayi* most closely resembles that of *Erebomaster* sp., although these species are only distantly related. A rivulose-microgranulate cuticular microstructure and a horizontal setal position are exhibited by both species. However, *Erebomaster* sp. exhibits neither an imbricate morphology nor any apparent micropores. The tubercles of *V. sayi* differ in shape and number from those of *Erebomaster* sp. A morphological gradient exists in the cuticular features of *V. sayi* which is illustrated by the progression from cephalothoracic tubercles to abdominal imbrications.

Eisner et al. (1971) reported leg dabbing as a defensive measure of *V. sayi*. This may indicate that the cuticle of this species does not function in dispersing defensive secretions since these chemicals are actively applied to the potential predator rather than diffusely disseminated over the dorsal integument to form a "chemical shield". A chemical shield is produced by the laniatorid *Stygnomma spinifera* (Packard) whose repellent secretions flow along lateral grooves of its dorsum, possibly by capillary action, before spreading over the dorsum (Duffield et al. 1981). The author has observed similar lateral grooves in an undetermined species of the Phalangodidae. No lateral grooves were observed on *Erebomaster* sp. in the present study. Although no live material was available for observations of the defensive behavior of *Erebomaster* sp., ventral grooves below the scent glands and hirsute segments of tarsi I are present. These leg dabbing characters are similar to those illustrated by Eisner et al. (1977) for two neotropical species of the Cosmetidae.

The cuticular morphology of *L. vittatum* to a great extent resembles that of its congener, *L. holtae*, and the confamilial *H. maculosus*. The dorsum of *L. vittatum* exhibits transverse and lateral bands which are devoid of tubercles and which were not observed in the other opilionids examined. Martens (1978) made reference to lateral "Kanalen" or channels on the surface of the opilionid integument which may function in dispering the secretion of the scent glands. The transverse and lateral bands observed in *L. vittatum* may function in dispersing its copious scent gland secretion. The size and morphology of the setae of *L. vittatum* are with few exceptions similar to those of *L. holtae, H. maculosus, E. nigrum, C. agilis*, and *H. kepharti*. Spicer (1987) illustrated a type of palpal mechanoreceptor (sensilla chaetica) from *Leiobunum townsendi* Weed that exhibits "whorled striae". Apparently, both sensory and non-sensory setae exhibit the spirally substriate morphology in *Leiobunum*, although additional species should be examined.

Only the absence of microgranulate transverse and lateral bands distinguishes *L. holtae* from *L. vittatum* in terms of cuticular morphology. Also, only the absence of denticles and cycloid facetodea may be used to distinguish *L. vittatum* and *L. holtae* from *H. maculosus*. Although various types of cycloid facetodea were observed in *V. sayi, Erebomaster* sp., *O. pictus*, and *C. agilis*, only those of *H. maculosus* are illustrated since they distinguish this species from *L. vittatum* and *L. holtae* in terms of cuticular microstructure. The function of these possibly glandular structures is unknown and histological studies are needed.

The cuticular morphology of *E. nigrum* is interesting because of the characteristic form of the tubercles. Cokendolpher (1980) referred to "obtuse tubercles scattered over the entire dorsum" in descriptions of the six species of *Eumesosoma*. The tubercular micropores observed in *L. vittatum, L. holtae, H. maculosus*, and *O. pictus* are not present in the confamilial *E. nigrum*. The setae of *E. nigrum* are similar in both size and structure to those of *L. vittatum, L. holtae, H. maculosus, C. agilis*, and *H. kepharti* but differ in that they are emitted from concave depressions atop the microareolae.

The microstructure of the integument of *O. pictus* is distinct because of its prominent laminar imbrications which cover the dorsum. The diversity in form of the laminae from the different cuticular regions of *O. pictus* demonstrates a morphological gradient. The tubercles of *O. pictus* resemble those of the confamilial *L. vittatum, L. holtae*, and *H. maculosus* since they exhibit micropores, but differ in that they generally are not covered by laminae.

The cuticular morphology of *C. agilis* is striking because of the numerous subdeltoid microtubercles and rugose abdominal integument. The imbricate morphology of the cephalothoracic region of *C. agilis* is in some respects similar to that of *O. pictus*, although these species are not closely related. The laminae of *C. agilis* are less prominent than those of *O. pictus* and are only seen in one area of its dorsum while in *O. pictus* they cover all regions. The diversity in the pattern of the microtubercles of *C. agilis* demonstrates a morphological gradient for this species. Shear (1975) described the dorsal cuticle of *C. agilis* as "soft and leathery without tubercles, spines, or prominent setae" in his taxonomic treatment of the Caddidae. Gruber (1974) referred to a soft cuticle with a finely granular, regularly arranged surface for *C. agilis*. The less sclerotized cuticle of *C. agilis* may, with further studies, be linked to the fact that this species is restricted to very humid, densely shaded habitats.

The cuticular morphology of *H. kepharti* is distinct because of the posteriorly oriented microtubercles and the relatively unornamented cuticular background. The setae of *H. kepharti* are similar to those of *L. vittatum, L. holtae, H. maculosus, E. nigrum*, and *C. agilis* but differ in that they are emitted from posterior microareolar margins at a 45 degree angle. Gruber (1970) does not specifically refer to the characteristic microtubercles of *H. kepharti* in his redescription of the species. Grainge and Pearson (1966) described a different cuticular morphology exhibiting numerous closely and regularly packed laminae in the related European species *Nemastoma lugubre* (Muller). Shear (1986) described and illustrated both the dorsal and ventral cuticular morphology of *Crosbycus dasycnemus* (Crosby) which he placed closest to *Hesperonemastoma* in his cladistic analysis of the Ceratolasmatidae. The numerous microtubercles (denticles) of the dorsal integument of *C. dasycnemus* resemble those of *H. kepharti* but were not illustrated at sufficient magnification for a detailed comparison. Shear also reported the presence of tridentate "scales" or cuticular processes on the ventral surface of *C. dasycnemus* which represents a marked difference in dorsal and ventral cuticular morphology. Although no descriptions of the ventral integument are given for the species in the present study, few differences in dorsal and ventral morphology were observed in specimens whose venters were examined, including that of *H. kepharti.*

Few descriptions of the function(s) of the opilionid integument have been reported other than its physiological ability to resist desiccation (Edgar 1971) and its role in dispersing scent gland secretions discussed above. Martens (1978) indicated that the integuments of representatives of the Trogulidae, Dicranolasmatidae, and Sclerosomatinae are strikingly glandular-papillose and that soil particles adhere to the secretions of these glands producing camouflauge. It is hoped that future studies will discover still other properties and functions of the opilionid integument and its secretions.

Only in recent years have taxonomic studies of opilionids included cuticular morphology as a character for analysis. Variations in integumental microstructure among families, genera, and species were used by Shear (1983, 1986) as characters for cladistic analysis. From the present study it is evident that the cuticular morphology of opilionids is a reliable character as long as adult specimens are examined, and may be used in addition to more traditional characters in systematic studies. I believe that the surface of the opilionid integument, just as Cooke and Shadab (1973) predicted for the ricinuleids, may possess a "considerable but largely untapped systematic potential."

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APPENDIX 1

Systematic list of the species included in this study. *=This species was determined to be near *Erebomaster acanthina* (Crosby and Bishop) but sufficiently distinct for new species status by Thomas S. Briggs of San Francisco, California.

Suborder Cyphophthalmi
  Superfamily Sironoidea
    Family Sironidae
      Siro exilis Hoffman
Suborder Laniatores
  Superfamily Gonyleptoidea
    Family Cosmetidae
      Vonones sayi (Simon)

Superfamily Travunoidea
Family Cladonychiidae
Erebomaster sp.*
Suborder Palpatores
Superfamily Phalangioidea
Family Phalangiidae
Subfamily Leiobuninae
Leiobunum vittatum (Say)
Leiobunum holtae McGhee
Hadrobunus maculosus (Wood)
Eumesosoma nigrum (Say)
Subfamily Oligolophinae
Odiellus pictus (Wood)
Superfamily Caddoidea
Family Caddidae
Caddo agilis Banks
Superfamily Ischyropsalidoidea
Family Ceratolasmatidae
Hesperonemastoma kepharti (Crosby and Bishop)

APPENDIX 2

Glossary of proposed morphological terms for describing the opilionid integument.

Acicular: needle-shaped; with a long, slender point as in certain setae.
Acute: sharply pointed; refers to laminar margins or other cuticular processes.
Alveolus, pl. alveolae: a small depressed or cup-like cavity; refers to setal insertions or sockets.
Arcuate: arched; setae that are curved like a bow.
Areole, pl. areolae: a pore-like depression; refers to insertions of certain setae within rounded microtubercles.
Deltoid: elongate-triangular as in certain cuticular processes; resembling the Greek letter delta with its apex extended.
Dentate: toothed, with tooth-like prominences.
Denticle: a tooth-like prominence; a general term.
Facetodea: cuticular structures composed of numerous small facets.
Foveolus, pl. foveolae: a minute pit or micropore.
Glabrous: smooth; devoid of any surface features.
Granulate: surfaces composed of small, obtuse to acute granules.
Imbricate: cuticular laminae that partially overlap as in roof shingles or fish scales.
Lamina, pl. laminae: cuticular layers, plates or scales that are generally imbricate.
Micro-: precedes terms describing features that measure 0.01 mm or less in size.
Mucronate: terminating in sharply pointed processes as in the margins of certain laminae.
Obtuse: blunt or rounded as opposed to sharply pointed.
Plicate: folded; impressed with striae to produce the appearance of having been folded or pleated.
Punctate: possessing circular, concave punctures or regular depressions.
Punctulate: finely punctate; with numerous small and closely set punctures or micropores.
Reticulate: superficially net-like or made up of a network of elevated, angular ridges; with surface ornamentation forming polygonal areas.
Rectilinear: in the form of a straight line as in certain setae.
Rivulose: exhibiting small, sinuate furrows or rivulets which are not parallel.
Rugose: wrinkled; refers to a pattern of impressed, irregular striae which are both parallel and intersecting producing a wrinkled appearance.
Sinuate: consisting of small sinuses; refers to wavy furrows of the integument.
Striae: narrow impressed lines or furrows of the integument which may be parallel or intersecting.
Sub-: below; somewhat; slightly; to a lesser degree than the term it precedes.
Torose: swollen; possessing superficial swellings or protuberances.
Tuberculate: exhibiting rounded, projecting protuberances which may possess a micropore.